COMPARING CONSEQUENCES OF CONSPECIFIC AND CONGENERIC COMPETITION FOR THE NATIVE *COCCINELLA NOVEMNOTATA* (COLEOPTERA: COCCINELIDAE)

A Thesis

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Master of Science

by

Rakim Turnipseed

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ABSTRACT

Three laboratory experiments were conducted to better understand the impact of an introduced coccinellid species, *Coccinella septempunctata* (C7), on a now rare native species, *C. novemnotata* (C9), which, since the mid 1980s, has undergone drastic declines following the establishment of the former. In the first experiment, larvae of C7 and two populations of C9 were reared interspecifically and intraspecifically (C9 only) in pairs through adult eclosion at two aphid prey densities. C7 reduced the survival and increased the time-to-adult eclosion of both populations of C9. Additionally, C9 survival began decreasing sooner interspecifically than intraspecifically. In the second experiment, C9 survival and adult weight increased as C9 became more mature in development to C7. In the third experiment, adult C7 consumed fewer eggs than did C9 but more of C9 than C7 eggs were consumed. Thus, not only is interspecific competition potentially a threat to C9, but also cannibalism of C9 eggs.

BIOGRAPHICAL SKETCH

Rakim was born in Los Angeles, CA on July 30, 1989. At the age of three he, his mother, and older brother relocated to Orlando, FL. Rakim grew up in Apopka, FL, a small suburb of Orlando. He attended Apopka Senior High School from which he graduated with honors in 2007, and where he would eventually meet his future wife. Following completion of high school Rakim attended and graduated from the University of Florida in Gainesville, FL in 2011. There he obtained a Bachelor of Science degree in Entomology and Nematology. Because he excelled in his major coursework and had received the opportunity to obtain research experience in a few different research labs, most notably as a Biological Science Aid for the U.S. Department of Agriculture, he decided to continue his studies in entomology at the graduate level. Thus, Rakim applied to and was accepted into several graduate programs including Cornell University, where he ultimately decided to attend in pursuit of the M.S. degree in Entomology. Upon completion of the degree requirements in fulfillment for the degree of M.S. at Cornell University Rakim will be heading to California to pursue a Ph.D. in Environmental Science, Policy, and Management at the University of California, Berkeley where he will continue working on an exotic/invasive arthropod species system.

This thesis is dedicated to my family, friends, and the Lost Ladybug Project.

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PREFACE

This thesis was written and formatted following the guidelines set forth by the Cornell University Graduate School. There are two chapters: Interspecific versus intraspecific competition between native and exotic ladybird beetle larvae (Coleoptera: Coccinellidae): *Coccinella novemnotata* versus *C. septempunctata* (Chapter 1) and Intraguild predation versus cannibalism on eggs of a native and exotic ladybird beetle (Coleoptera: Coccinellidae): *Coccinella novemnotata* versus *C. septempunctata* (Chapter 2).

Interspecific versus intraspecific competition between native and exotic coccinellid larvae (Coleoptera: Coccinellidae): *Coccinella novemnotata* versus *C. septempunctata*

Abstract

Since the 1980s, the formerly common native ninespotted lady beetle, *Coccinella novemnotata,* has decreased rapidly in population density and geographic range in North America. This decline closely follows the establishment and spread of the non-native sevenspotted lady beetle, *C. septempunctata.* In this study, larvae of two populations of *C. novemnotata* were reared both intraspecifically and interspecifically with *C. septempunctata* at varying aphid prey densities to determine if the introduced species has an effect on survival and/or development of the native species. Results show that *C. septempunctata* negatively affected the survival of both "eastern" and "western" populations of *C. novemnotata*, regardless of aphid density. The "eastern" population of *C. novemnotata* had a higher adult weight in the presence of another "eastern" conspecific at the high aphid density, but this did not translate to a higher weight compared to "western" *C. novemnotata* when both were paired with *C. septempunctata* larvae. In a separate experiment, initiated with paired larvae of varying ages, results show that *C. novemnotata* survival increased as it became more mature in development relative to *C. septempunctata*. The weight of adult *C. novemnotata* increased when the initial larvae were started at a higher larval instar. These results suggest that interspecific competition with *C. septempunctata* may negatively affect the fitness of *C. novemnotata*, but that the intensity of this impact may vary based across *C. novemnotata* populations and may be dependent of the local phenology of the two species.

Introduction

Although introduced coccinellid or lady beetle species can provide effective control of pest populations (Debach and Rosen 1991), a substantial proportion of introduced species (Stiling and Simberloff 2000) pose such detrimental effects on native species that they are considered invasive (Yasuda et al. 2004). The native species impacted by introduced coccinellids can range from non-target herbivores that are consumed to native predators that are affected by competition (Elliot et al. 1996). Non-target herbivores include native aphids (Hesler 2012) and larvae of native lepidoptera such as *Danaus plexippus*, the monarch butterfly (Koch 2003). Predators impacted by introduced lady beetle species include native lady beetle species (Obrycki at al. 1998).

Losey et al. (2012) suggest five possible non-exclusive mechanisms for negative interactions between introduced and native coccinellids; intraguild predation, scramble competition for prey, competition for non-prey resources, the introduction of parasitoids or pathogens, and hybridization. In this study we focus on the potential role of the first two mechanisms, competition for prey and intraguild predation. The magnitude to which these interactions occur is potentially heightened by the trend towards larger body sizes in invasive species compared to native species within the same guild (Roy et al. 2002; Evans et al. 2011; Losey et al. 2012), a characteristic likely allowing the former to overpower the latter during an aggressive interaction or to consume prey more rapidly. These competitive interactions are thought to lead to the exclusion of the weaker species from a guild (Gakkhar et al. 2007), a phenomenon known as the competitive exclusion principle; in the case of competition between a native and an exotic species, the native

species is often the weaker competitor or intraguild prey (Yasuda et al. 2004). This effect may potentially explain the decline of native ladybird beetle species (Coleoptera: Coccinellidae) in the United States following the rapid spread of coccinellids from other countries since the 1980s, potentially leading to a decrease in efficacy of ecosystem services provided by these beneficial species (Snyder 2006). While introduced species often provide beneficial ecosystem services such species are less likely to be adapted to extreme environmental conditions that may ensue in an invaded habitat (Burgiel and Muir 2010), which could lead to the loss of introduced species, in addition to those native species lost via competition.

Several studies have addressed the potential impact of introduced coccinellids on native species and the results have been mixed. In a study in which the invasive species *Harmonia axyridis* Pallas was paired with the North American species *Adalia bipunctata* Linnaeus, the latter exhibited slower development than when placed with a conspecific (Kajita et al. 2000). Similarly, in a laboratory test in which *Coccinella undecimpunctata* Linnaeus, a species native to the Azores, and *H. axyridis* were placed together the former laid fewer eggs in the presence of the latter than when alone (Soares and Serpa 2007). This effect was also demonstrated on *A. bipunctata* by both *H. axyridis* and the introduced *C. septempunctata* in a study by Kajita et al. (2006a).

Conversely, several other studies did not find an impact of introduced on native species. In a study by Evans (1991) it was shown that when *Hippodamia convergens* Guérin-Méneville, a native coccinellid to the U.S., and the non-native *C. septempunctata* Linnaeus, were reared both interspecifically and intraspecifically there was no significant difference in competition between these treatments. Similarly, results from another study

showed that the body size of the native coccinellid *Coleomegilla maculata* De Geer did not decrease following the establishment of *C. septempunctata* (Obrycki et al. 1998b). In a laboratory study, Yasuda et al. (2004) demonstrated that neither of two North American species, *C. transversoguttata richardsoni* Brown and *H. convergens*, exhibited a change in development time or weight when placed with *H. axyridis* or *C. septempunctata* than when paired with their respective conspecifics. Similarly, in a field cage study by Hoogendorn and Heimpel (2004) it was shown that *H. axyridis* did not affect the survival or weight gain of *C. maculata*.

While it is generally thought that exotic species often inflict detrimental ecological effects on native species the above studies show that the former species do not always outcompete the latter species when given the opportunity (Sato and Dixon 2004; Yasuda et al. 2004). Additionally, the literature on competition between native and exotic coccinellids is lacking in studies involving the effects of exotic coccinellids on the once very abundant North American species, *C. novemnotata* Herbst. This species was once among the most abundant coccinellids present in the continental U.S., as well as portions of Canada, before the mid-1980s (Gordon 1985). In fact, it was the most dominant coccinellid species present in the northeastern region of the U.S. at the time (Gordon 1985). It served as an important biological control agent in the suppression of pest populations, such as aphids and other soft-bodied arthropods, in different crops including potatoes, cotton, corn, alfalfa, soybeans, and arboreal habitats (Harmon et al. 2007). Due to the high ecological value and cultural significance it had *C. novemnotata* was honored as the official state insect of New York (Harmon et al. 2007). However, in the mid 1980s populations of *C. novemnotata* began drastically declining to near extinction following

the establishment of *C. septempunctata,* the seven spotted lady beetle, from Europe and several studies have suggested that the establishment and spread of *C. septempunctata* was an important cause of *C. novemnotata'*s decline (Wheeler and Hoebeke 1995; Losey et al. 2012).

Previous studies of *C. novemnotata* have established that adult beetles recently collected from the western US are significantly smaller than their offspring reared in the laboratory and the historical mean size of this species (Losey et al. 2012). The authors suggest that these relationships are consistent with the expectations arising from potential prey limitation by *C. septempunctata*. Additional studies (Lai and Losey, unpublished, 2011) demonstrate that when *C. novemnotata* larvae are reared with *C. septempunctata* larvae at a single prey density, they have significantly lower survival than *C. novemnotata* larvae reared in conspecific pairs. Since several studies (Polis et al. 1989; Lucas et al. 1998; Yasuda et al. 2004), have demonstrated that the strength of interactions between larvae of native and exotic species depends on several factors, including prey availability and developmental stage of the larvae we expand on previous studies on the interaction of *C. novemnotata* and *C. septempunctata* by including these factors. In addition, since size has been shown to be an important factor in competitive interactions, and a population of *C. novemnotata* was discovered in New York that featured a significantly larger body size than those from western populations, we compare all factors between these two groups. Our specific objective was to assess the potential impact of *C. septempunctata* on *C. novemnotata* by quantifying the survival and development of two populations of *C. novemnotata* reared in both conspecific and interspecific pairs across a range of prey densities, and initial developmental stages

Materials and Methods

Two experiments were conducted to delineate further the impact of *C. septempunctata* (C7) on *C. novemnotata* (C9) fitness. In the first experiment two populations of C9 from different regions were paired intraspecifically and interspecifically with C7 of the same age to determine differences in effects on fitness by C7 on the two populations of C9. In the second experiment C9 was paired interspecifically with C7 at different ages to ascertain the influence maturity to C7 has on C9 fitness. For the following studies, larvae of C9 and C7 were obtained from eggs reared in colony within a laboratory setting. The eggs were obtained from adults that had been collected from Oregon, South Dakota and New York. *C. novemnotata* adults, and eggs laid by them, collected from Oregon and South Dakota were designated as the Western population (C9W). Those from New York were designated as the Eastern population (C9E). There was no such designation between C7 regional populations as Losey et al. (2012) did not report a difference in average body size between current populations of C7 and those of historical specimens. Larvae of both species were reared to the necessary instar stage in an incubator at 22 ± 1 °C with a RH level of 75 ± 5% and L16:D8 photoperiod. The arena in which the pairs were reared consisted of a clear plastic cup (22.8 mm x 54.9 mm). All specimens were fed equal amounts of a diet solely comprised of the pea aphid, *Acyrthosiphon pisum* Harris, and the green peach aphid, *Myzus persicae* Sulzer (Hemiptera: Aphididae). Aphids were reared in colony on plants of the fava bean, *Vicia faba* L. (Fabales: Fabaceae).

Experiment 1: Conspecific and heterospecific pairings of first instar C9 and C7

In this study we paired in each arena a first instar C9 (C9W or C9E) with either a coetaneous (of the same age) C7 or C9 to evaluate whether C7 reduces the fitness of C9 more than does a conspecific. The focal species of interest was C9 not C7. The experiment involved eight treatment pairings, including two aphid prey density levels: two conspecific C9E on a diet of 40 aphids, one C9E and one C7 on a diet of 40 aphids, two conspecific C9E on a diet of 20 aphids, one C9E and one C7 on a diet of 20 aphids, two conspecific C9W on a diet of 40 aphids, one C9W and one C7 on a diet of 40 aphids, two conspecific C9W on a diet of 20 aphids, and one C9W and one C7 on a diet of 20 aphids. The high and low aphid density levels take into account that an individual coccinellid reaches optimal fitness (time-to-adult eclosion and fecundity) on a diet of 21 aphids per day (Kopco 2011, unpublished). Thus, providing a pair of coccinellids with either a diet that should discourage (40 aphids) and encourage (20 aphids) competition was essential to simulate decreasing food resources. We analyzed 30 replicates of each intraspecific pairing (n=120) and 60 replicates of each interspecific pairing (n=240) for a total of 360 (n=360) replicates (Table 1.1a). Replicates were set up across three to four different blocks (days). Pairs were reared through adult eclosion. ANOVA was used to determine if there were any main or interaction effects on C9 adult weight and C9 time-to-adult eclosion. Tukey's HSD test was run to identify such effects if they existed. A Chi-square test was run using logistical regression to evaluate significant differences in C9 survival to adult eclosion across treatments.

Table 1.1a. Illustration of treatments for intraspecific and interspecific pairings of *Coccinella novemnotata* and *C. septempunctata*

Partner Species	Prey Density	C9 Origin	# of Rows
C9	40	East	30
C9	20	East	30
C9	40	West	30
C9	20	West	30
C7	40	East	60
C7	20	East	60
C7	40	West	60
C7	20	West	60

Table shows Eastern C9 paired with a sympatric conspecific on a diet of 40 aphids (n=30), eastern C9 paired with a sympatric conspecific on a diet of 20 aphids (n=30), western C9 paired with a sympatric conspecific on a diet of 40 aphids (n=30), western C9 paired with a sympatric conspecific on a diet of 20 aphids (n=30), eastern C9 paired with C7 on a diet of 40 aphids (n=60), eastern C9 paired with C7 on a diet of 20 aphids (n=60), western C9 paired with C7 on a diet of 40 aphids (n=60), and western C9 paired with C7 on a diet of 20 aphids (n=60).

At each daily observation of each replicate cup we recorded whether the larvae had died or eclosed. For each case in which a larva died (except one replicate in a C9 conspecific pairing) it was clear that predation had occurred either because the dead larva was missing completely or parts of it had been consumed. Therefore, death was attributed to cannibalism (conspecific pairing: C9+C9) or intraguild predation (heterospecific pairing: C9+C7).

For each treatment combination the following variables were assessed: 1) average C9 adult weight, 2) average time-to-adult eclosion of C9, 3) daily percent survival of C9, and 4) total percent of C9 surviving to adult eclosion (Note: for the conspecific C9 treatments

one of the two individuals was selected randomly each day to serve as the focal species for the purposes of data collection as there was no method for discerning between the two specimens). Adults were weighed 24 hours after eclosion to allow for hardening of the elytra.

Experiment 1: Statistical Analyses

To compare adult weight and time-to-adult eclosion of C9 (focal species) between the eight treatments we ran a multi-factor ANOVA using the following independent variables: aphid prey density, regional origin of C9 (East or West), and partner species (conspecific C9 or heterospecific C7). Following this test we performed Tukey's HSD test on means to identify significant differences between treatments. The graphs for daily percent survival of C9 were generated based on data from Kaplan-Meier analysis.

Experiment 2: Heterospecific pairings of C9 and C7 at developmentally staggered instar levels

In this study we paired in each arena C9 and C7 of different ages to evaluate the influence of C9 maturity to C7 on C9 fitness. Because the first experiment illustrated the most negative effects on C9W (rather than C9E) by C7 we used only C9W in this study. The experiment involved the use of 12 treatments: 1) a first instar C9W paired with a second instar C7 or "$C9W_{1st}$+$C7_{2nd}$" (n=20), 2) a first instar C9W paired with a first instar C7 for control or "$C9W_{1st}$+$C7_{1st}$" (n=35), 3) a second instar C9W with a first instar

C7 or "$C9W_{2nd}$+$C7_{1st}$" (n=20); 4) a second instar C9W with a second instar C7 or "$C9W_{2nd}$+$C7_{2nd}$" (n=24), 5) a third instar C9W with a first instar C7 or "$C9W_{3rd}$+$C7_{1st}$" (n=20), and 6) a third instar C9W with a second instar C7 or "$C9W_{3rd}$+$C7_{2nd}$" (n=21); each of these treatments were exposed to an aphid diet of density 40 and 20 for a total of 12 treatments.

As in the previous experiment we observed daily for mortality or eclosion. In all cases of mortality it was due to intraguild predation as there was a complete absence of the intraguild prey. In other words, the disappearance of a specimen was counted as having been a victim of intraguild predation.

For each treatment combination we assessed average C9W adult weight and total percent of C9 surviving to adulthood in each treatment.

Experiment 2: Statistical Analyses

To compare average C9W adult weight across the 12 treatments a multifactor ANOVA was ran using the following independent variables: prey density, C9W (focal species) instar level, and C7 (partner species) instar level. Following this we performed Tukey's HSD test on means to identify significant differences between treatments.

Results

Experiment 1

We obtained data from logistical regression survival analysis (i.e., 2x8 contingency table) to construct a table (Table 1.1b) detailing the final overall survival of C9 under each of

the eight treatment levels. We found there was an interaction effect of partner species by C9 origin on the final percent of C9 surviving to adult eclosion. Specifically, we found that the "western" population of C9 in competition with C7 exhibited a significantly lower mean percent survival to adult eclosion at both aphid densities of 40 and 20 (27% and 15%, respectively) than did the "eastern" population of C9 in the presence of C7 (std err=0.1319; ChiSquare=6.03; p value = 0.0140). Additionally, regardless of aphid density or C9 origin, C9 survival was reduced to 31% on average when paired with C7 from 75% when reared with a conspecific (std err=0.1319; ChiSquare=63.49; dF=7; p value < 0.0001).

Table 1.1b. Percent of *Coccinella novemnotata* ("C9"), from two regions of origin ("Eastern" and "Western"), surviving to adult eclosion under intraspecific and interspecific competition with *C. septempunctata* ("C7") at two aphid prey densities ("40" and "20").

Partner Species	Prey Density	C9 Origin	Number of Rows	# C9 Alive	Percent Alive
C9	40	Eastern	30	24	80%
C9	20	Eastern	30	19	63%
C9	40	Western	30	25	83%
C9	20	Western	30	21	70%
				Average:	75%
C7	40	Eastern	60	32	54%
C7	20	Eastern	60	18	30%
C7	40	Western	60	16	27%
C7	20	Western	60	9	15%
				Average:	31%

We obtained data from Kaplan-Meier analyses to construct a graph showing the daily percent survival of C9 at each of eight treatment levels (Figures 1.1a and 1.1b): 1) C9 from the eastern population reared with a sympatric conspecific, 2) C9 from the eastern population reared with a heterospecific C7, 3) C9 from the western population reared with a sympatric conspecific C9, and 4) C9 from the western population reared with a

heterospecific C7; each of these treatments were ran at two aphid prey densities (40 or 20) for a total of eight treatments. At both aphid densities we found that C9W reared with a C7 exhibited a decrease in daily percent survival sooner than all other treatments. Those specimens that either died before adult eclosion or reached adult eclosion were censored and excluded from continued daily percent survival analysis. This approached was continued until all C9s either had died or reached adult eclosion at which point the study was complete.

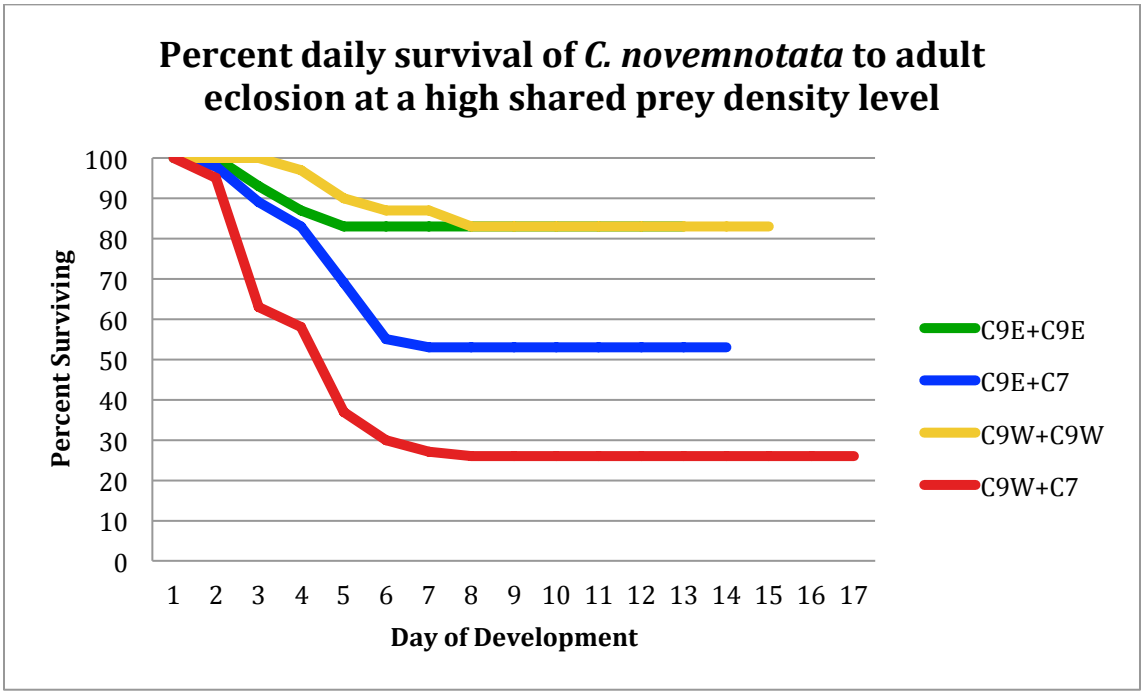

Figure 1.1a. Percent of *Coccinella novemnotata* from two populations ("C9E" signifies the Eastern population; "C9W" signifies the Western population) surviving each day under intraspecific and interspecific pairing with *C. septempunctata* at the high aphid prey density of 40.

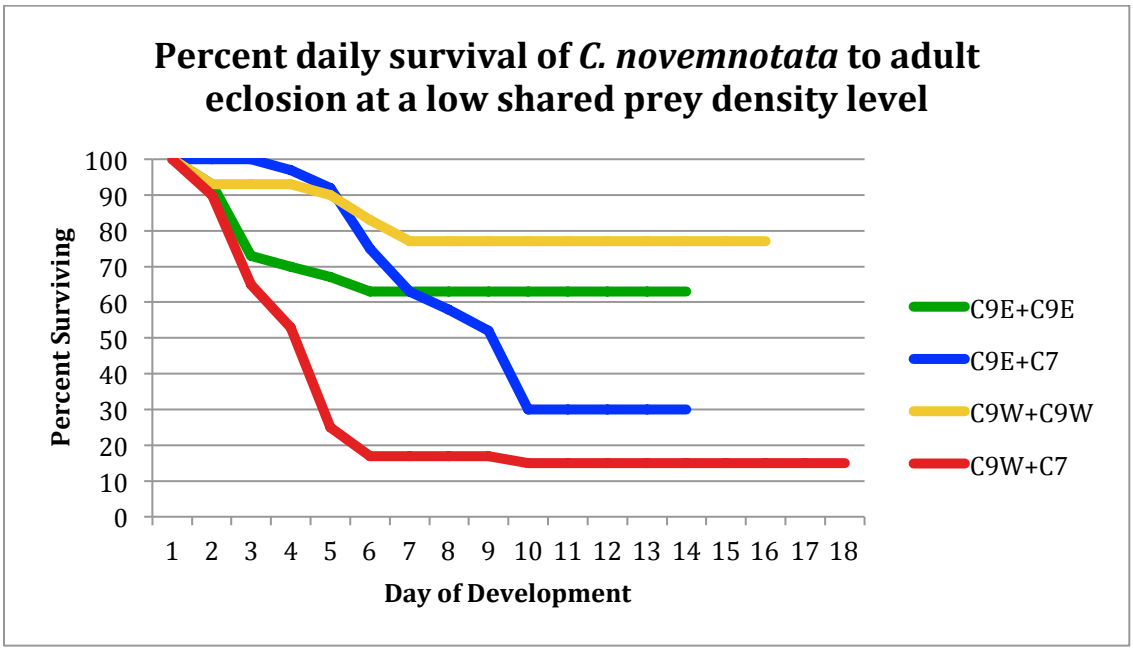

Figure 1.1b. Percent of *Coccinella novemnotata* from two populations ("C9E" signifies the Eastern population; "C9W" signifies the Western population) surviving each day under intraspecific and interspecific pairing with *C. septempunctata* at the low aphid prey density of 20.

In most cases mortality of C9 reared interspecifically with C7 could be attributed to intraguild predation by C7 given that the body of the former would either be eaten to some extent or non-existent (Figures 1.2a-c). Cannibalism among C9 did occur but was a rare event (Figure 1.2d).

Figure 1.2a. A third instar *Coccinella septempunctata* larva feeding on a third instar *C. novemnotata* larva.

Figure 1.2b. A fourth instar *Coccinella septempunctata* larva having consumed the majority of body mass of a third instar *C. novemnotata larva*.

Figure 1.2c. A third instar *Coccinella septempunctata* larva having chewed through the cuticle of a third instar *C. novemnotata* larva.

Figure 1.2d. A third instar *Coccinella novemnotata* larva feeding on a second instar conspecific larva.

An ANOVA revealed no three-way interaction between the factors of aphid prey density ("40" or "20)", partner species (conspecific "C9" or "C7"), and C9 origin ("East" or "West") on mean total number of days to C9 adult eclosion (Table 1.2). However, ANOVA revealed significant two-way interaction effects of aphid prey density by partner species and partner species by C9 origin. Following these analyses we performed Tukey's HSD test for each of these two interaction effects to identify those treatments in which C9 exhibited a significantly different total number of days needed to reach adult eclosion. For the interaction effect of aphid prey density by partner species it was found that C9 in the presence of C7 at the low aphid prey density of 20 required the longest amount of time to reach adult eclosion compared to all other treatments (14.1 days, std err = 0.419277984, N rows = 27, F ratio = 6.36, p value = 0.0127). For the interaction effect of partner species by C9 origin it was found that C9W in the presence of a C7 required the longest amount of time to reach adult eclosion compared to all other treatments (14.88 days, std err = 0.643739078, N rows = 25, F ratio = 7.45, p value = 0.0069).

Table 1.2. A table showing the mean total number of days required for two populations ("East" or "West") of *Coccinella novemnotata* ("C9") to reach adult eclosion under intraspecific and interspecific pairings with *C. septempunctata* ("C7") at aphid prey densities of "40" and "20" individuals. There were significant two-way interaction effects of prey density by partner species and partner species by C9 origin.

Partner	Density	C9 Origin	N Rows	Mean Total Days to Eclosion
C9	40	East	25	11.6
C9	20	East	19	11.6
C9	40	West	25	12.5
C9	20	West	21	13.0
			Average:	12.2
C7	40	East	32	11.7
C7	20	East	18	13.1
C7	40	West	16	14.1
C7	20	West	9	16.2
			Average:	13.8

An ANOVA revealed no three-way interaction effect between the factors of aphid prey density, partner species, and region of C9 origin on mean C9 adult weight (Table 1.3). An ANOVA did reveal that there were significant two-way interaction effects of aphid prey density by partner species and partner species by C9 origin on mean C9 adult weight. Following these analyses we performed Tukey's HSD test for mean C9 adult weight across treatments. It was found that C9 in the presence of a conspecific C9 at the high aphid prey density of 40 individuals reached a significantly higher adult weight compared to all other treatments (0.0269 grams, std err = 0.00074401, N rows = 49, F ratio = 3.8838, p value = 0.00505). It was found that C9E in the presence of a sympatric conspecific reached a significantly higher adult weight compared to all other treatments (0.02695 grams, std err = 0.000799848, N rows = 49, F ratio = 1.7473, p value = 0.01881).

Table 1.3. A table showing the mean adult weight for two populations ("East" or "West") of *Coccinella novemnotata* ("C9) under intraspecific and interspecific pairings with *C. septempunctata* ("C7") at aphid densities of "40" and "20" individuals. There were significant two-way interaction effects of prey density by partner species and partner species by C9 origin.

Partner	Density	C9 Origin	N Rows	Mean Adult Weight (g)
C9	40	East	24	0.0282
C9	20	East	19	0.0247
C9	40	West	25	0.0255
C9	20	West	21	0.0213
				Average: 0.0249
C7	40	East	32	0.0227
C7	20	East	18	0.0206
C7	40	West	16	0.0203
C7	20	West	9	0.0215
				Average: 0.0213

Experiment 2

Data was obtained from logistic regression survival analyses to construct a table (Table 1.4) and graph (Figure 1.4) detailing the final overall survival of C9W under each of the 12 treatment levels. It was found that there were no three-way interaction effect of aphid density, C9W instar level, and C7 instar level on the percent of C9W surviving to adult eclosion. However, single main effects were observed of C9W instar level (std err=167.11, ChiSquare=114.036; p-value = 0.0001) and C7 instar level (std err=167.11; ChiSquare=10.574; p-value=0.0011) on the percent of C9W surviving to adult eclosion. It was found that at both the high and low aphid prey densities C9W survival to eclosion was significantly higher in the combination involving a third instar C9W paired with a first instar C7 (100% and 95%, respectively).

Table 1.4. Percent of *Coccinella novemnotata* (Western population = "C9W") surviving to adult eclosion when paired with *C. septempunctata* (C7) of different instar stages at high and low aphid prey densities of "40" and "20" individuals, respectively. Main effects of C9W instar level and C7 instar level were observed. Instar level of each of the two species is underscored to the right of the species name abbreviation under the "Treatment" column.

Treatment	Aphid Density	Total # C9	# C9 Survived	N Rows	% C9 Survival
$C9W_{1st}+C7_{2nd}$	40	20	3	20	15%
$C9W_{1st}+C7_{2nd}$	20	20	1	20	5%
					Average: 8%
$C9W_{1st}+C7_{1st}$	40	35	12	35	34%
$C9W_{1st}+C7_{1st}$	20	35	7	35	20%
					Average: 27%
$C9W_{2nd}+C7_{2nd}$	40	20	14	20	70%
$C9W_{2nd}+C7_{2nd}$	20	20	11	20	55%
					Average: 63%
$C9W_{2nd}+C7_{1st}$	40	24	19	24	79%
$C9W_{2nd}+C7_{1st}$	20	24	19	24	79%
					Average: 79%
$C9W_{3rd}+C7_{1st}$	40	20	20	20	100%
$C9W_{3rd}+C7_{1st}$	20	20	19	20	95%
					Average: 98%
$C9W_{3rd}+C7_{2nd}$	40	21	20	21	95%
$C9W_{3rd}+C7_{2nd}$	20	21	15	21	71%
					Average: 83%

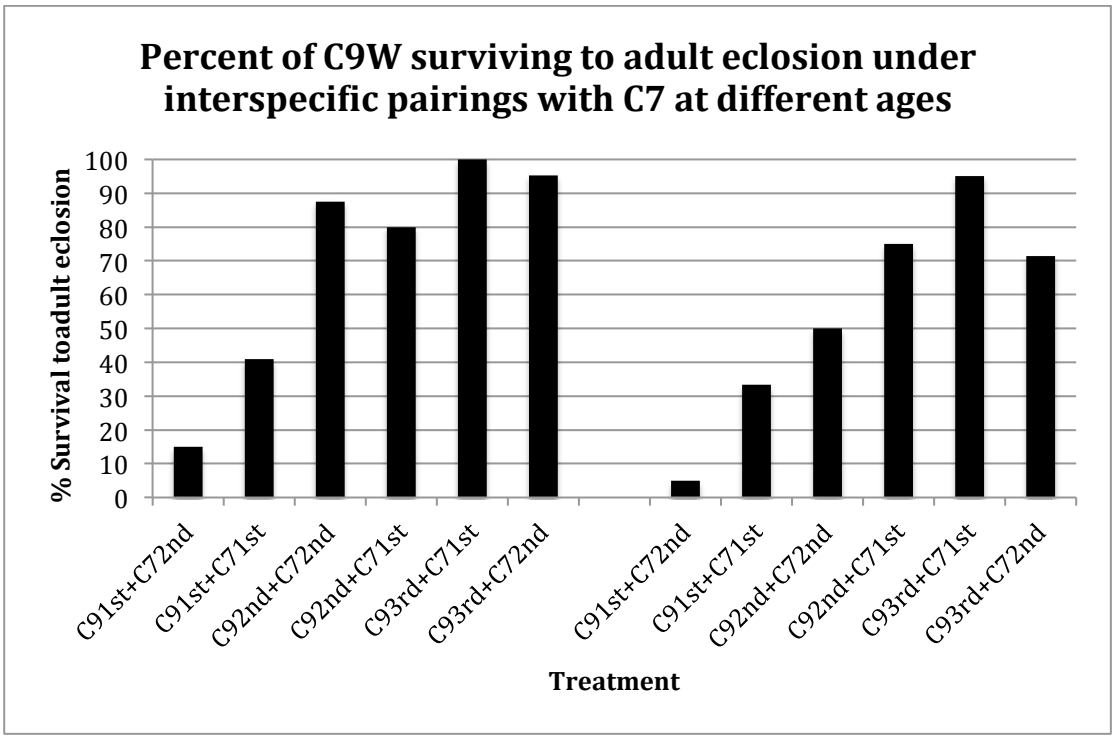

Figure 1.3. Percent of *C. novemnotata* (Western population) survival to adult eclosion when paired with *C. septempunctata* at different instar stages, at high and low aphid prey densities. Bars to the left represent pairs reared on a diet of 20 aphids; those on the right represent pairs reared on a diet of no aphids. Instar level of each of the two species is found to the right of the species name abbreviation.

Data analysis revealed no three-way interaction effect between focal species instar, partner species instar, and aphid density on C9 adult weight, though we did find that the instar level of C7 served as a single main effect (Table 1.5). No two-way interaction effects were observed either. We found that third instar C9s paired from the onset with younger C7s reached a significantly higher adult weight than did C9s of younger instar levels (0.0257 grams, N rows = 42, std err = 0.0008759, F ratio = 8.0188, p value = 0.0005). We were not able to statistically analyze the adult weight of C9 from the combination of a first instar C9 paired with a second instar C7 as mortality of the former was too high.

Table 1.5. Adult weight of *Coccinella novemnotata* ("C9") under interspecific pairings with *C. septempunctata* ("C7") of different instar stages at high and low aphid prey densities. Main effect of C7 instar level was observed.

C9 Instar	C7 Instar	Aphid Density	N Rows	C9 Adult Weight (g)
1	2	40	20	0.0201
1	2	20	20	0.0208
				Average: 0.0204
1	1	40	35	0.0237
1	1	20	35	0.0224
				Average: 0.0230
2	1	40	20	0.0269
2	1	20	20	0.0245
				Average: 0.0257
2	2	40	24	0.0239
2	2	20	24	0.022
				Average: 0.0229
3	1	40	20	0.0283
3	1	20	20	0.0283
				Average: 0.0283
3	2	40	21	0.0242
3	2	20	21	0.0221
				Average: 0.0231

Discussion

In the first study we observed that pairing *C. novemnotata* with a conspecific at the limited aphid prey density and pairing it with *C. septempunctata*, regardless of aphid prey density, resulted in an increase in the number of days it took *C. novemnotata* to reach adult eclosion and a decrease in adult weight of *C. novemnotata.* These results may suggest that interspecific competition is stronger than intraspecific competition. Because mean time to adult eclosion and mean adult weight did not significantly differ between the heterospecific pairings and the conspecific pairing (at the low prey

density), this suggests *C. novemnotata* could be equally negatively affected by conspecific and heterospecific coccinellids at the field level if prey densities are extremely limited. Final percent survival to adult eclosion in *C. novemnotata* was at its lowest under interspecific rather than intraspecific pairings, in large part due to high rates of intraguild predation of *C. novemnotata* by *C. septempunctata;* this occurred more frequently than those much rarer events in which *C. novemnotata* cannibalized a conspecific. As in the case of prey densities being extremely limited, predation of *C. novemnotata* by *C. septempunctata* could potentially help to explain the decline of the former in the U.S. since the 1980s if similar results are exhibited at the field level. These results were expected based on several studies including one by Yasuda et al. (2004), which showed that competitive interactions between coccinellid species favored the exotic over the native species, which may not have as high of voracity or reproductive fitness as the former.

In the second study we observed that pairing *C. novemnotata* of a higher instar with a lower instar *C. septempunctata* increased the survival of the former. Additionally, an increase in *C. novemnotata* adult weight was observed when it was reared beginning at the third instar stadium with *C. septempunctata* at the first instar stadium. We expected these results given that larger competitors should compete better once reaching a certain point in size than younger competitors demonstrated by Yasuda et al. (2004), from which it was found that survival of indigenous species, *C. transversoguttata* and *H. convergens*, increased when they and introduced species, *C. septempunctata* and *H. axyridis*, were reared together at the fourth instar level versus the second instar level, and that survival of the indigenous species decreased as the

instar level of their non-native partners increased. Similar results were found in other studies involving coccinellid species (Obrycki et al. 1998a; Michaud 2002; Sato et al. 2003; Snyder et al. 2004) as well as studies involving arthropods of other species (Lucas et al. 1998; Rosenheim et al. 1999; Hindayana et al. 2001). However, there have not been adequate interactive studies between the two species *C. novemnotata* and *C. septempunctata* largely due to the rarity of *C. novemnotata* populations in the field.

Future studies should involve testing at the field level for the effects observed in this study, as natural settings are most realistic. It would also be important to ascertain whether potentially competition at the field level impacts biological control efforts. While introduced coccinellid species tend to do well at reducing pest populations, such as aphids, it remains unclear how their presence impacts biological control efforts when native species are outcompeted or fall victim to intraguild predation by these introduced species. Finally, future studies should test for these effects when *C. novemnotata* is paired with an introduced species other than, or in addition to, *C. septempunctata*, such as *H. axyridis.* While it is believed that *C. septempunctata* may potentially be the initial cause of the decline of *C. novemnotata*, *H. axyridis* has been shown to be aggressive and strongly competitive against several species of native coccinellids (Leppanen 2012). Thus, understanding how it competes against *C. novemnotata* compared to how *C. septempunctata* competes with *C. novemnotata* would be worth investigating. Such information would suggest whether or not *H. axyridis* might have contributed to keeping *C. novemnotata* populations at low levels after initial declines caused by *C. septempunctata*.

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Intraguild predation versus cannibalism on eggs of a native and exotic ladybird beetle (Coleoptera: Coccinellidae): *Coccinella novemnotata* versus *C. septempunctata*

Abstract

The ninespotted ladybird beetle, *Coccinella novemnotata,* has undergone precipitous declines in population density across the United States following the establishment of the sevenspotted ladybird beetle, *C. septempunctata*, in the mid 1980s. Some potential mechanisms by which these declines may have occurred include interspecific and intraspecific competition between these two species, and more specifically, intraguild predation and cannibalism of each other's eggs. In this study we compared the relative frequencies of cannibalism and intraguild predation on eggs between these two species at aphid densities of 20 and zero individuals. We found that 1) *C. novemnotata* consumed more eggs than *C. septempunctata*, irrespective of egg species and aphid density; 2) *C. novemnotata* eggs were consumed more frequently than *C. septempunctata* eggs, irrespective of predator species and aphid density; and 3) more eggs were consumed when no aphids were included in the arena, irrespective of predator and egg species.

Introduction

Exotic species that have been introduced into countries for ecosystem services, such as biological control, have proven to provide long-term control of targeted pest populations (van Lenteren 2006); van Driesche at al. 2008). However, as a consequence of these introductions such species also have the potential to negatively

impact the environment as they may detrimentally affect other organisms (Williamson 1996; Gurevitch and Padilla 2004; Smith 2012; Babendrier 2007; De Clercq et al. 2011). For example, exotic species may cause the decline of native species within the same guild via direct or indirect competitive interactions, though these specific types of interactions are not always discernable (Pimentel et al. 2005; Snyder and Evans 2006; Crowder and Snyder 2010). One example of a direct interaction thought to contribute to the decline of native species by exotic species is intraguild predation, the consumption of an organism by another within the same guild. Intraguild predation is an extreme form of competition between species (Polis et al. 1989) and is thought to occur when extraguild prey of native and exotic competitors become extremely limited (Musser and Shelton 2003; Cottrell 2005).

Intraguild predation can be symmetrical or asymmetrical. Symmetrical intraguild predation would involve two species within the same guild preying upon each other equally, and asymmetrical intraguild predation would involve one species being the dominant predator of another species within the same guild (Polis et al. 1989). Intraguild predation is thought to affect the interactions of different predators and their prey (Snyder 2009) and thus, it is of concern as to whether or not this phenomenon negatively affects biological control efforts in agricultural systems (Vance-Chalcraft et al. 2007) and whether it potentially contributes to widespread decline of native species (De Clercq et al. 2011). Furthermore, however, it has been suggested by Janssen et al. (2006) that such an effect on biological control efforts is unlikely.

Several exotic coccinellid species in the U.S., including *Harmonia axyridis* and *Coccinella septempunctata*, are known to exhibit intraguild predation on native coccinellids (Snyder et al. 2004; Cottrell 2005). Following the introduction of these species were drastic declines in native coccinellid populations and it is widely suggested that intraguild predation on native coccinellids by introduced coccinellids

has contributed to the declines of the former (Evans 1991; Obrycki et al. 1998; Cottrell and Yeargan 1999; Kajita et al. 2000; Michaud 2002). Additionally, it is suggested that predation on native coccinellid eggs is a phenomenon contributing to these declines (Cottrell and Yeargan 1998a).

Intraguild predation of coccinellid eggs is exhibited most frequently by other coccinellids than other organisms (Cottrell 2007), potentially because many coccinellid eggs are chemically defended, allowing coccinellid predators to detoxify them more readily (Hemptinne et al. 2000). In a laboratory study Cottrell (2004, 2005) demonstrated that *H. axyridis* was able to complete development to adult eclosion solely on a diet of certain native coccinellid species, but the reverse was not observed by those native species on a diet of *H. axyridis* eggs. However, Hemptinne et al. (2000) demonstrated that the exotic *C. septempunctata* was more reluctant to eat the eggs of the native *Adalia bipunctata* than the reverse.

Another less suggested mechanism that could drive native species declines is cannibalism, whereby an animal consumes another of the same species (Meisner et al. 2011). Among the Coccinellidae, cannibalism is responsible for many instances of mortality (Hironori and Katsuhiro 1997). Dixon (2000) demonstrated that cannibalism in fact reduces juvenile survival significantly in coccinellids. However, it is suggested that in some species coccinellid cannibals obtain a high-quality diet from their conspecific prey and are able to detoxify their conspecific prey more readily (Snyder et al. 2000). For example, Snyder et al. (2000) showed that *H. axyridis* achieved higher survival and a reduced time to adult eclosion on a diet of conspecific prey than aphids of poor quality. In another study, Jafari (2013) demonstrated that egg cannibalism by the larva of a coccinellid species, *Hippodamia variegata* Goeze, proved advantageous to its fitness. However, in a study by Hemptinne et al. (2000) it was demonstrated that *C. septempunctata* took longer to develop on a diet of

conspecific eggs versus aphids, although the study found that *C. septempunctata* survival was higher when fed either of these than when fed on a diet of *A. bipunctata* eggs. Thus, the effect of cannibalism on the fitness of a coccinellid species deserves more attention. It is suggested that cannibalism could be detrimental to biological control efforts using coccinellids because the number of conspecific prey may be too high to nutritional benefits derived from consuming such prey (2013). This potentially may help to explain the decline in native lady beetle populations if cannibalism is observed frequently enough at large field scales.

Understanding the relative frequency of intraguild predation to cannibalism of native coccinellid eggs and factors that influence these phenomena are of importance, as such information would provide some additional insight into the decline of native coccinellid populations. In a study by Randoni et al. (2012) it was demonstrated that intraguild predation incidences between native and exotic species were not any higher than incidences of cannibalism among native and exotic species involving *H. axyridis*, *C. septempunctata*, and *Adalia bipunctata*. Additionally, Cottrell (2005) showed that extraguild prey availability affects egg predation in some Coccinellidae; when aphid densities were increased predation on eggs decreased. Thus, in this study we aimed to ascertain whether or not, in the presence or absence of aphids, the relative frequencies of intraguild predation and cannibalism on eggs differ between the exotic *C. septempunctata* and a rare native species, *C. novemnotata*, one that Randoni et al. (2012) did not work with in their study.

Materials and Methods

Eggs of two populations of C. novemnotata (C9E = “Eastern” population, C9W = “Western” population) and *C. septempunctata* (C7) were obtained from adults reared

in colony. C9E adults were obtained from New York while C9W adults were obtained from Oregon and South Dakota during collection trips. C7 was obtained from all three states. A single adult beetle of either of the two species was starved for 24 hours prior to the study after which point it was placed in a clear plastic cup arena (22.8 mm x 54.9 mm). A cluster of three eggs from each of the two species was placed into each arena on opposite sides. In each arena, either 20 aphids were added or no aphids were added. Thus, the treatments were as follows: 1) a single C9 adult with 20 aphids, 2) a single C9 adult with no aphids, 3) a single C7 adult with 20 aphids, and 4) a single C7 adult with no aphids. Each adult in each arena was exposed to three conspecific eggs on one side of the arena and three heterospecific eggs on the other side of the arena. Each arena contained a folded moistened piece of paper towel (1.5 mm x 0.5 mm) single leaf of the fava bean plant, *Vicia faba* L (Fabales: Fabaceae). Aphids used in this study were the pea aphid, *Acyrthosiphon pisum* Harris, and the green peach aphid, *Myzus persicae* Sulzer (Hemiptera: Aphididae). Aphids were reared in colony on plants of *V. faba*.

Replicates were observed across three different blocks (dates) and each observation was set for two hours. At the end of each observation period the total number of eggs of each species consumed by the adult beetle was recorded. No adults died during the study. We analyzed the data by using egg species, predator species, and aphid density as independent variables in ANOVA. We then performed Tukey's HSD test to identify differences in the mean number of eggs consumed across treatments.

Results

No three-way interaction effect was found between predator species, egg species, and aphid density (F ratio = 1.7322; p value = 0.1902) (Table 2.1, Figure 2.1). Additionally, we found no two-way interaction effects. However, there were single main effects for all three of independent variables on the number of eggs consumed in each species. It was found that C9 consumed more eggs than C7, not taking into account the egg species or aphid density (1.27 eggs; N rows = 80; F ratio=6.3925; p value=0.0125; std error=0.1293) (Figure 2.2). It was found that C9 eggs were consumed more than C7 eggs, not taking into account predator species or aphid density (1.225 eggs; N rows=80; F ratio=3.927; p value=0.0493; std error=0.1293) (Figure 2.3). It was found that more eggs were consumed when no aphids were present in the arena than when 20 aphids present, not taking into account predator or egg species (1.4375 eggs; N rows=80; F ratio=18.5331; p value=0.0001; std error=0.1293) (Figure 2.4).

Table 2.1. Total number of *Coccinella novemnotata* (“C9”) and *C. septempunctata* (“C7”) eggs consumed by adults of each species at aphid densities of “20” and “0” individuals. Single main effects of predator species, eggs species, and aphid density were each observed.

Predator Species	Egg Species	Aphid Density	# Eggs Eaten	Tukey's Test
C9	C9	20	1.55	A B
C9	C7	20	0.5	A B C
C7	C9	20	0.45	B C
C7	C7	20	0.1	C
C9	C9	0	1.6	A
C9	C7	0	1.45	A B
C7	C9	0	1.3	A B
C7	C7	0	1.4	A B

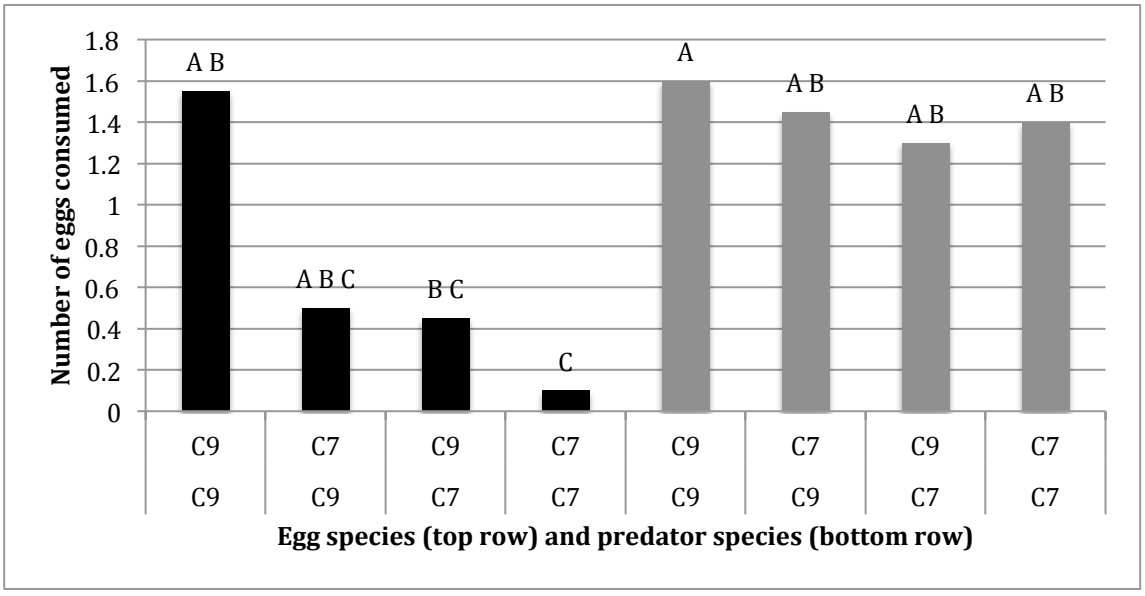

Figure 2.1. Total number of *Coccinella novemnotata* (“C9”) and *C. septempunctata* (“C7”) eggs consumed by adults of each species at aphid densities of “20” (black bars) and “0” (grey bars) individuals. Single main effects of predator species, eggs species, and aphid density were each observed.

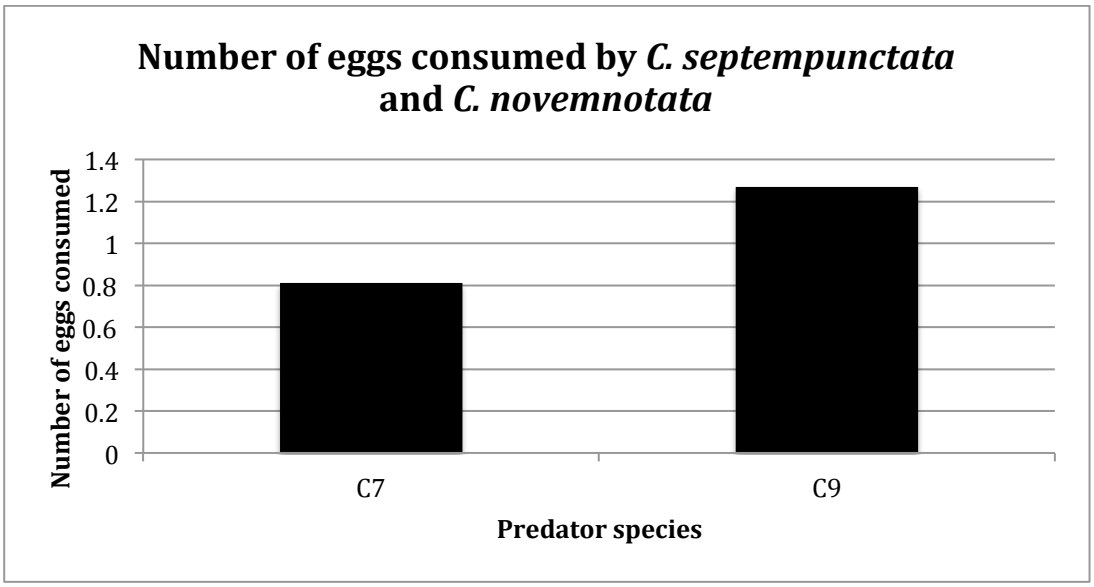

Figure 2.2. Total number of eggs consumed by *Coccinella septempunctata* ("C7") and *C. novemnotata* ("C9") adults, not taking into account egg species and aphid density.

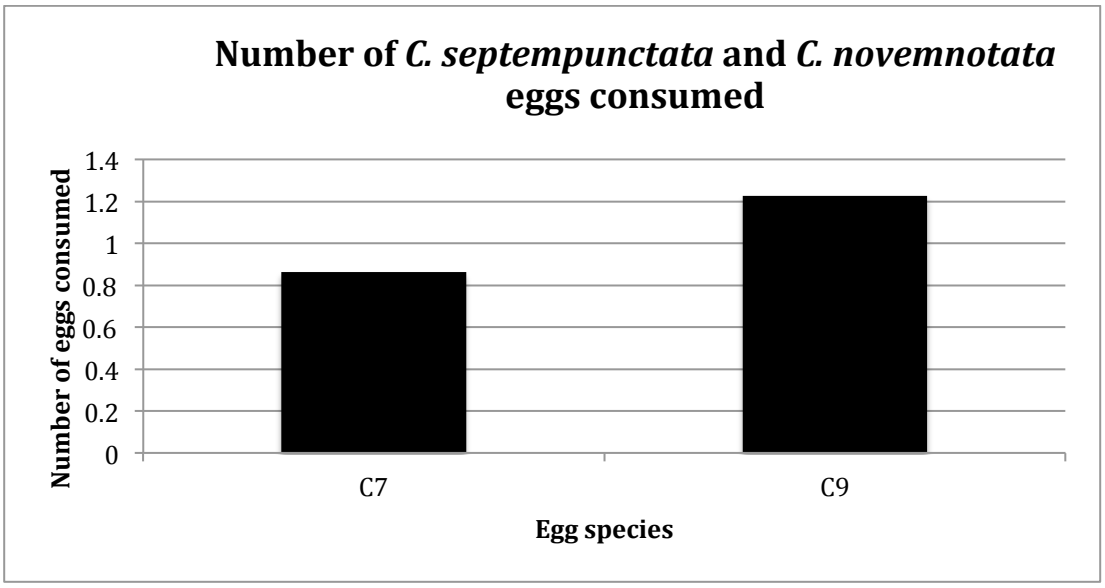

Figure 2.3. Total number of *Coccinella septempunctata* ("C7") and *C. novemnotata* ("C9") eggs consumed, not taking into account predator species and aphid density.

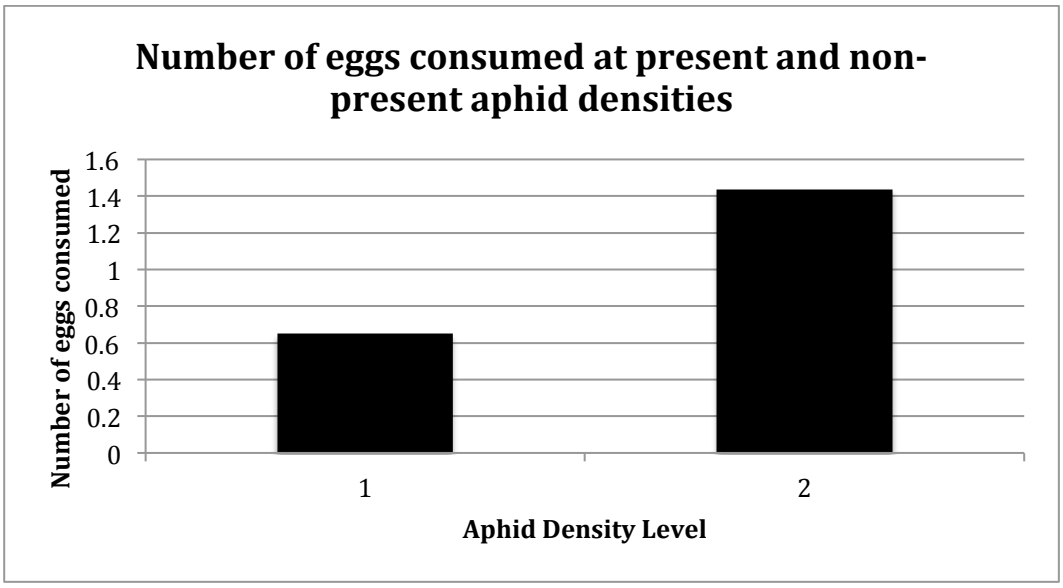

Figure 2.4. Total number of eggs consumed when 20 ("1") or zero ("2") aphids were present in the arena, regardless of predator and egg species.

Figure 2.5. *Coccinella septempunctata* having consumed two of three conspecific and heterospecific eggs with no aphid prey.

Figure 2.6. *Coccinella novemnotata* in the presence of aphids and unconsumed conspecific and heterospecific eggs.

Discussion

The results from our study do not agree with the study by Agarwala and Dixon (1992) whereby they showed that *C. septempunctata* and *A. bipunctata* were more likely to eat conspecifc eggs than those of each other. In our study, neither of the two coccinellid species were more likely to consume a heterospecific egg than a conspecific egg. Similarly, they were not more likely to consume a conspecific egg than a heterospecific egg, even when no aphids were present. We observed, however, that more *C. novemnotata* eggs were consumed than *C. septempunctata* eggs. This could potentially be the result of *C. novemnotata* eggs not being as high in alkalinity as *C. septempunctata* eggs.

Coccinellids are known to have alkaloids of different toxicities (Agarwala and Dixon 1992), which may potentially explain the above observation if *C. septempunctata* eggs are more toxic than *C. novemnotata* eggs. For example, Hemptinne et al. (2000) demonstrated that *A. bipunctata* contains one additional alkaloid compound than *C. septempunctata*, which was commensurate with their results showing that *A. bipunctata* predation on *C. septempunctata* eggs occurred at a higher frequency than the reverse. Hemptinne et al. (2000) notes that more studies are needed testing the effect of coccinellid toxicity on intraguild predation.

Lady beetles are not thought to feed on diets comprised only of conspecific or heterospecific eggs in the field. However, when aphid densities become low coccinellids may be more likely to consume eggs. Because cannibalism of conspecific eggs has been reported to be more nutritious than intraguild predation of eggs (Hemptinne et al. 2000), and due to the fact that introduced coccinellids are often believed to be more successful at foraging for aphid prey in the presence of native competitors, cannibalism of eggs of native species potentially exists at higher frequencies in the field than intraguild predation of eggs.

The results from this laboratory study may shed light onto the widespread decline of C. novemnotata beginning in the 1980s following the establishment of *C. septempunctata*. Since many species consume conspecific prey when extraguild prey densities become limited it is possible that this phenomenon occurred throughout the U.S. among *C. novemnotata* populations as *C. septempunctata* outcompeted the native species for shared prey resources.

Future studies should ascertain the effect of other independent variables that affect consumption of coccinellid eggs such as life stage (i.e., adult, first instar, second instar, third instar, and fourth instar), time since last feeding, rearing origin (i.e., lab-reared versus field-collected). According to Hemptinne et al. (2000) and Osawa (1992), starved coccinellids, particularly larvae, should exhibit increased feeding on eggs. As aphid availability becomes more limiting due to exploitative competition by exotic species cannibalism could potentially become more of a threat to native species given that conspecific eggs tend to be more nutritious to a predator than heterospecific eggs (Hemptinne et al. 2000). Future studies should look for this effect at larger spatial scales.

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